

THE CONSTITUTION OF THE GASTROPOD PROTO-
CONCH: ITS VALUE AS A TAXONOMIC FEATURE
AND THE SIGNIFICANCE OF SOME OF ITS
FORMS.*

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(Communicated by Dr. H. G. Chapman.)

(Plate i.)

INTRODUCTION.

In August, 1905, I read, before this Society, a paper on "The Onotogenetic Stages represented by the Gastropod Protoconch" (30). The more important portion of this paper had been forwarded to the editors of the *Quarterly Journal of Microscopical Science* about six months previously, and was published in that journal in October of the same year (32).

Since penning those papers—which were themselves the outcome of over four years' study of the Gastropod Protoconch, as represented in a collection, such as falls to the good fortune of but few to study—I have subjected the theories and opinions therein put forward to thoughtful criticism from time to time, and have collected further notes on the subject. Our knowledge of the Protoconch has also been enriched in the interval by many contributors, taxonomists describing new species, and my own contributions have aroused criticism, favourable and otherwise. These contributions, and my own recent studies in comparative Zoology and Physiology, permit me to review the subject from a broader standpoint, and at the same time to treat some of its aspects in more detail. Meanwhile, during the five years which I have devoted to these other subjects, I have to a certain extent lost touch with general Malacology, and must on

*Submitted as a Thesis for the degree of D.Sc., to the Faculty of Science of the University of Sydney, in 1911.

this score beg the indulgence of my readers, if it be found that my nomenclature is out of date, and in view of the rapid and manifold changes which historical research has of recent years imparted to the face of Conchological literature, I fear that this may be the case.

THE CONSTITUTION OF THE PROTOCONCH.

The terms "Protoconch" and "Apex" are used here, as in my last communication (30, 32), to designate those few early whorls of the shell which differ in some marked character or characters from the succeeding structure. It was in those papers maintained that, as thus defined, the Protoconch may have been formed "during one or more of four ontogenetic stages." In accordance with this view I recognised four components in an ideally perfect Protoconch, and for these I offered the following names and definitions (30, p. 327):—

1. *Phyloconch*.—This is the "primitive" shell of Lankester (35). It is formed by almost every member of the phylum, but, with rare exceptions, it is shed at an early stage, and does not enter into the composition of the protoconch.

2. *Velococh*.—The greater portion of this is formed during the *Veliger* stage, though it may have been begun just before that stage.

3. *Nepioconch*.—This is formed during the *Nepionic* stage, but, for reasons given in a previous paper (29), I am inclined to regard it as of rare occurrence.

4. *Ananeoconch*.—Formed during early *Neanic* stages."

The formation of the Phyloconch cannot be assigned to any definite stage in the life-history. In *Limnea stagnalis* the primitive shell-gland is still in the form of a pit in the early *Veliger* stage (Lankester); in *Patella* the shell-gland has opened out, and a shallow thimble-shaped shell is present in the *Trochosphere* (Patten); whilst in many Lamelli-branchs, the pit-like shell-gland appears in the *Gastrula*, e.g. *Ostrea virginiana* (Brooks). In the first case it is *Typembryonic*, in the last *Metembryonic*, using those terms

in the sense that Jackson proposed them (23). In some cases the primitive shell-gland is never functional.

Instead of *Teloconch*, the term *Nectoconch* would have been more applicable. I had failed to realise, when the term was proposed, how constantly the thimble-shaped symmetrical nucleus is formed by the *Trochosphere*. I now substitute the term *Nectoconch*, and define it as "that portion of the protoconch which is formed during the pelagic existence of the embryo, or the equivalent stages in the case of species such as all *Pulmonata*, which have no pelagic existence." Or more precisely "that portion of the protoconch formed after the flattening out of the primitive shell-gland, and before the loss of the velum." In the case of most, if not all, *Audibranchs* this is the only shell formed.

Before the *Nepioconch* can be discussed, it is necessary to define the *Nepionic* stage in the *Gastropoda*.

Throughout the whole animal kingdom, it is possible to recognise embryonic and postembryonic divisions of the life-history. In the great majority of cases, we can also recognise juvenile (*Neanic*) and adult (*Ephetric*) stages in the post-embryonic division, and in many instances the acquisition of new or loss of established characters defines a stage of Old Age (*Gerontic*). The occurrence of sexually mature larvæ (*Axolotl*, *Aphidæ*, etc.), in no way lessens the value of the generalisation, but serves only to point the necessity of care in its particularisation.

Again, in the vast majority of cases we can recognise a typical larval stage, and one or more pre-larval stages [Jackson recognises four (23)] in the Embryonic division of the ontogeny. And here again, the occasional apparent or real suppression of one or more of these stages emphasises the need for care in the application of any nomenclature arising out of the generalisation.

In all those cases where larval organs are developed, a period of metamorphosis will intervene between the larval

(Phylembryonic) stage and adolescence. This metamorphosis will always involve changes leading to the loss of the larval organs, and may or may not involve others leading to the acquisition of adult structures. In the absence of larval organs there may yet be a metamorphosis leading to the acquisition of adult characters only, such is almost the case in many Entomostraca. We are thus able to recognise, in very many instances, five distinct stages in the life-history of the individual, and in some cases a sixth:—

1. Pre-larval	... Up to and including Jackson's	} Embryonic.
	<i>Typembryo</i> .	
2. Larval	... <i>Phylembryo</i> (Jackson).	} Post-Embryonic.
3. Metamorphosis...	<i>Nepionic</i> (Buckman & Bather's name).	
4. Juvenescence	... <i>Neanic</i> (B. & B.).	
5. Prime of Life	... <i>Ephebic</i> (B. & B.).	
6. Old Age	... <i>Gerontic</i> (B. & B.).	

In many cases, these stages are so merged, that, to define them, is much like attempting to divide the thin from the thick end of the wedge, the whole life-history taking the form of a gradual evolution. In some cases, the whole metamorphosis is passed through and *juvenescence entered upon* before the loss of the larval organs; for instance, in the *Mammalia*, where the last portion of intra-uterine life, two to three months in the human species, is potentially juvenescent, and may be made actually so by premature birth.

Difficulties present themselves more especially in the identification of the early stages, and these difficulties of application will, I fear, make it well-nigh impossible to give always the same value to Jackson's terms for the subdivision of the embryonic stage. The *Phylembryo*, however, should always be identifiable, as the last definitely embryonic stage, and is represented by many characteristic larval forms.

The attempt has been made, in one or two instances, to define the stage of development by reference to the time of liberation from the maternal organism, or escape from the

egg, and has led to very fallacious conclusions. That this method of determination is entirely unreliable, is illustrated by the following facts. In most fishes, the ova are shed before fertilisation, but, in many of the sharks and rays, the offspring are born as fully-formed young; whilst, in others of the Selachians, the fertilised ovum is deposited in the early stages of segmentation enclosed in a horny shell. The great majority of the Amphibia deposit eggs, and the young go through a free tadpole stage; two Salamanders are viviparous, and, in one of these, the young are liberated in the form of the adult, as also are the young of *Pipa americana*. Most Reptilia are oviparous; one or two Lacertilians and Ophidians are ovoviviparous. It follows, then, that no generalisation may be made on ontogenetic stages, which takes as its basis the period of hatching or liberation by the maternal organism.

It is unsafe to found identifications on the presence or absence of specific characters; this practice has also led to errors. To the Ornithologist, the unsegmented ovum would be specifically recognisable, by its shell; in fact, in nearly all cases, the ova may be identified by the specialist; they already bear specific characters.

Buckman and Bather (4) defined the *Nepionic* stage as that *immediately succeeding the embryonic stages*, and during which no specific characters make their appearance; and the next, or *Neanic* stage, as that during which specific characters and all other morphological features present in the adult, appear and undergo development. Even if, as is probable, these authors meant specific characters of *the adult organism*, the definitions are not capable of general application; there are instances among the Gastropoda where they fail to lead us right; and throughout the whole of the Amniota, practically all the specific characters of the adult are developed before the loss of the larval organs.

In view of the fact that the degree of development of the different organs and systems of organs is subject to wide

variation, it seems that some character must be chosen arbitrarily and used as a datum-line from which to measure the stages on either side. Thus we find that, in one group, one system is far advanced, whilst others are but as yet only indicated; in another group we find this system in an early stage of development, whilst others are far advanced, so that it is impossible to offer a general definition of any of the early ontogenetic stages, in terms of the degree of general development. These varieties of degree of development affect even the earliest stages; in some of the Entomostraca histogenesis commences very early. Hacker (12) was able to recognise the endo-mesomeres in the eight-celled stage in *Cyclops*; I have myself recognised them in the sixteen-celled stage of an undescribed species allied to *Ive*; and they were recognised in the thirty-two celled stage in *Uetochilus* by Grobben (33); whilst, in many other crustacea, histogenesis is not apparent till much later stages. The condition of the primitive shell-gland of Mollusca above referred to, is another illustration of this point.

It seems that, in the larval organs, we have the character or set of characters, whose retention may be arbitrarily chosen as the recognition-mark of the embryo as distinct from the adult. Such a definition is unnatural in as far as it does not define any particular stage of development, for, in some organisms, the larval organs are aborted very early, and, in others, as already mentioned, not till potential adolescence, yet it is no more artificial than any other definition based on the degree of development of any other organ, and no general definition is possible which would include all organs. This definition is, on the other hand, a natural one, in one important respect; the retention of the larval organs is, in the vast majority of cases, attended by an environment or mode of life differing markedly, and, in some cases, almost fundamentally, from that of the organism after the loss of the organs in question. In point of fact, this definition is in conformity with common usage.

If it be granted that the organism is still a *Phylembryo* so long as it is in possession of the larval organs, then the succeeding or *Nepionic* stage may be defined as "that during which the larval organs are aborted or shed." Such a definition is of perfectly general application; by it the *Nepionic* stage in the Ascidians, Amphibians, Lepidoptera, Nemer-teans, etc., is immediately made recognisable.

As a particular form of this definition applicable to the Gastropoda, I have proposed the following (29): "That stage during which the velum undergoes degeneration and (more or less completely) disappears." The stage is not generally recognisably represented in the protoconch, and this fact calls for special comment; but before proceeding to this question, the following extracts from Korschelt and Heider (34, p. 133) are given as illustrating the absence of any necessary relationship between this stage and the escape of the embryo from egg or maternal organism.

"The *perfectly* developed *Veliger* larva is found almost exclusively among the marine Gastropoda, the young of which swim about freely for a long time. Among fresh-water Gastropoda *Neritina* passes through a stage with a well-developed bilobed velum resembling that of *Vermetus*, but the *Veliger* larva does not live a free life, but passes through the stage within the egg-capsule. When the embryo leaves the egg-capsule it shows the adult form." "*Onchidium*, a Pulmonate living between the tide marks . . . while still within the egg-capsule becomes a *Veliger* larva with a coiled snell and a large bi-lobed velum." "The velum may still persist after the foot has attained a considerable size, and when the development of the other organs is also far advanced, but it gradually diminishes in size and finally degenerates, the larva thereby passing over into the adult form which, indeed, had already been nearly approached."

That *Paludina* is viviparous, and that most Gastropoda deposit the eggs immediately on fertilisation is so well known as to need no special quotation. In *Patella* "the egg-envelope

is thrown off very early, even while cleavage is still going on'' (*loc. cit.*, p. 124.)

The retention of the velum is very much protracted in some species of *Triphora*, which have been obtained as *Veliger* larvæ with "several whorls of the adult shell formed." The other extreme is presented by those Pulmonata with transient and poorly-developed Velum.

Turning now to the very constant absence of the *Nepioconch* as a recognisable constituent of the *Protoconch*. It must be clearly understood that this term is applicable not to some particular portion of the protoconch but to any portion formed during a particular period in the life-history of the species, namely, the period of transition from embryo to juvenescence, during which the velum becomes aborted. Owing to the variation in the degree of development of other organs at the time of abortion of the velum, the *Nectococonch* may be formed entirely by the undifferentiated ectoderm of the visceral hump, or in part also by a free mantle-fold, and moreover may be either corneous or calcareous. The *Nepioconch* when recognisable, or, in fact, whenever present, is formed by a free mantle-edge, and consequently may be either corneous or calcareous like the *Nectococonch*.

In the case of very many marine gastropoda, the length of retention of the velum is probably to some extent conditioned by the length of the pelagic existence; once the larva comes to rest, the velum is probably rapidly aborted. The *Veliger* of *Umatium* is undoubtedly pelagic, but young specimens having but one half whorl of adult structure added to the *Nectococonch* have lost all trace of the velum. Two main types of *Nectococonch* are recognisable, the one corneous, the other calcareous. In the former case, together with the abortion of the velum, there is, during the nepionic stage, a change in the mode of functioning of the mantle: under these conditions one would expect the secretory activities of the shell-gland to be in abeyance. As a matter of fact, we usually find that there is an abrupt change from the corneous *Necto-*

conch to a calcareous sculptured structure which is, in miniature, the same as the adult shell. I regard this last as the *Ananeanoconch*, and believe that there is no *Nepioconch* present.

In the case of species in possession of a calcareous shell during the *l'eliger* period, we almost invariably find that there is a varix formed around the peristome of the *Nectoconch*, and the succeeding structure is similar to the adult shell. The assumption of a benthic existence is here, as in the last case, followed by the rapid abortion of the velum, and the varix marks the nepionic pause in growth, is in fact the *Nepioconch*.

In some few cases, however, the prolonged retention of the velum is such as to allow of the complete development of the mantle-edge and all other organs during the planctonic existence, so that when the benthic existence is entered upon, there is no recognisable pause in growth; the *Nepioconch*, present in these cases, is not recognisable because of its similarity to the preceding and succeeding shell-structure.

In all those forms which pass the whole of the *l'eliger* stage within the egg-capsule, the whole embryonic history might, in its uneventfulness, be depicted graphically by an even unbroken curve; and our problem is to explain why, in view of the unvarying environment, any of the ontogenetic stages should be represented by differentiated shell-structure, rather than to explain why all are not so represented. A quotation from Lankester (35), which I have used before (30), may be aptly used again here:—" . . . we may speak of primary, secondary and tertiary shells in molluscs, recognising the fact that they may be merely phases fused by continuity of growth so as to form but one shell, or that, in other cases they may be presented as separate individual things, in virtue of the non-development of later phases, or in virtue of sudden changes of the mantle surface causing the shedding or disappearance of one phase of shell-formation before a later one is entered upon." I have elsewhere (29)

laid stress upon the importance of change in environment or functional activity in producing those differences, which enable one to define the constituents of the *Protoconch*. The change in environment probably acts to bring about the change in functional activity which, it is conceivable, was potentially present, and only in abeyance in the absence of the necessary environment. Thus it is possible that, in the species referred to above, the power to secrete a calcareous shell was already present in the free-swimming *Veliger* with a horny shell, but was in abeyance owing to the absence of calcium salts in a form which might be assimilated. Within the egg-capsule, the only factors which will vary the form of the shell are changes in the form and functional activity of the mantle or other shell-secreting surface. Changes in the mantle may be abrupt and productive of sudden change in the shell-characters, or may be gradual, the shell changing *pari passu*. The abortion of the velum, *per se*, need not be productive of any shell-characters; it is not accompanied by any change in environmental conditions, such as would possibly be reflected in functional changes. If, however, all the Gastropoda be evolved or descended from forms with pelagic larvæ, and the universal occurrence of *Trochosphere* and *Veliger* causes this to be generally conceded; then it is conceivable that, even in those forms which now pass those stages within the egg-capsule, the abortion of the velum is marked by a pause in growth, and occurs at the same time as the acquisition of adult characters by the mantle, since such is the case in nearly all species with pelagic larvæ at present.

The conclusions of this section may be summarised as follows:

In the ontogeny of the great majority of the members of the animal kingdom there is a period when organs characteristic of a larval stage are aborted; and since, in many cases, this period is also marked by other important morphological and physiological changes, it is advisable to designate this period always by the same name. The term *Nepionic* pro-

posed by Buckman and Bather, is the correct term to use. In the Gastropod mollusc this stage is characterised by the abortion of the velum, but in the majority of cases, the reduction and disappearance of this organ is very rapid, or is unattended by other variants, so that no recognisable conchylaceous record of the stage is left in the protoconch; nevertheless it probably corresponds in point of time with the abrupt change which so commonly marks the protoconch off from the true conch. Finally, it is concluded that, in most cases, the early portions of the true conch are formed during early juvenescence, that, in fact, they are *Ananeanic structures*.

THE VALUE OF THE PROTOCONCH AS A TAXONOMIC FEATURE AND THE SIGNIFICANCE OF SOME OF ITS FORMS.

The value of any feature for taxonomic purposes depends on its immunity from variation under circumstances which phylogenetically may be regarded as extraneous; or, stated in another way, only those characters which reflect phylogenetic relationships may be safely used for taxonomic purposes, and it is almost axiomatic that those most liable to variation are the most untrustworthy.

If it be found that any given feature has been so little affected by the phylogenetic history of the organisms possessing it, that it fails to show modifications corresponding to the major groups into which those organisms are divisible; and if, further, it be shown that this character is plastic to its environment, that feature is surely hardly trustworthy as a guide to the division of the major into minor groups. Such a feature as this is the Gastropod Protoconch.

Perrier and Gravier (42) have maintained that Tachygenesis is the constant mode of action of heredity, that, in effect, all continuous evolution consists in the development of the new characters in successively earlier and earlier stages in the ontogeny of the successive generations. The same idea is contained in the law of Serres, which has been more

explicitly put by Fritz Müller and Haeckel in the statement that the ontogeny of an organism is a recapitulation of its phylogeny. There are certainly many characteristic phases in the ontogeny, especially of the higher animals, finger-posts, which point the road that has been travelled, but these records constantly fail us when we look for information as to the more recent stages in the journey. Thus, in the ontogeny of the Horse, we find no *Eohippus* stage; in that of birds, no *Hesperornis* or *Ichthyornis* stage. In the Platypus, on the other hand, we find traces of a toothed ancestor in the ontogenetic records; and among invertebrates, in *Cymatium parkinsonianum* we find abundant trace of the sculptured ancestor, *C. torirostris*, in the early whorls (see later, p. 74). It is to be noted, however, that in all those cases where trace of some recent ancestor is preserved in the record, it is present at a time when the organism is practically or actually in possession of all the adult features.

In general, it may be stated that only the complete adult organism is sufficiently strong to leave an impress upon the embryonic ontogenetic record. Thus the reptilian affinities of the Aves are recognisable in the ontogeny, but not so the teeth of a more recent ancestor. To state a hypothetical case, suppose that a branch of the Gastropoda should become so modified as to no longer be classed with the Mollusca, we would expect to find traces of its molluscan ancestry in its ontogeny, but it is possible that its origin from the Gastropoda would not be clear, and it is highly improbable that from the ontogenetic record we should be able to place the ancestors as Opisthobranchs, Prosobranchs or Pulmonates. It seems, then, that strong though the power of retention of ancestral features may be, it is insufficiently strong to retain permanently any trace of those minor fluctuations which have undoubtedly occurred in the evolution of the species; conversely, strong though the tachygenetic tendencies may be to modify the ontogeny of an organism, it is not until they affect the whole organism in a fundamental manner that they

leave a lasting impress. If this were not so, our classifications of the members of the different phyla would be far more perfect, more natural than they are. As an illustration of this, we can confidently say that the species of *Onchidium* are recently evolved from some marine ancestor, but though an Opisthobranch origin has been suggested, there is not sufficient evidence to decide whether the ancestor was Opisthobranch or Prosobranch; we continue to class them with the Pulmonata, though by no means satisfied that they are derived from the same stock as other Pulmonates. This group (Pulmonata) then, is probably at least diphyletic, and may be polyphyletic.

If we imagine a feature "A" to be acquired by an adult organism, say a gastropod, during a given period "a," that character appearing late in life on the ultimate whorl of the adult shell, then, in the succeeding period "b," this character will have been, by tachygenetic tendencies carried back on to the penultimate whorl, and, in the period "c," appears on the antepenultimate whorl, and so on. Finally, however, this minor tachygenetic wave will break against a rock, and be eliminated from the ontogenetic record. The rock against which it breaks is the hereditary resistance of the larval stages. It is this resistance of the larval stages which has preserved with, but minor modifications, the *Trochosphere* stage in the ontogeny of the Rotifera, the Annulata, and the Mollusca, and the *Veliger* in that of all Gastropoda. In some cases, the adult organism has proven equally resistant, and there has resulted the "persistent type," e.g., *Lingula*.

The morphological features of the gastropod, like those of most other larvæ, are stable, and have been beyond the reach of those minor fluctuations which have resulted in the differentiation of the various subdivisions of the group. (It may be suggested that the extreme reduction of the velum in some of the Pulmonata, shadowing forth, as it does, its approaching elimination from the ontogenetic record of these forms, indicates that the *Veliger* ancestor was a completely

organised mollusc, so that, if represented without modification in the recent fauna, its representatives would probably form a group of similar value to the Thecosomatous Pteropoda.)

Notwithstanding their phylogenetic immutability, the *Veliger* and indeed also the *Trochosphere* larvæ present quite obvious differences among themselves, as also do their *Nectocoenchs*; and the questions naturally arise: To what are these differences due? And are they not taxonomically significant?

The second question must be answered in the negative, certainly as concerns the *Nectocoench*, and probably also the larva within it. Since tachygenesis impressed the *Veliger* upon the ontogenesis, its waves have broken against a rock of resistance to variation so strong at this stage that fundamentally all the larvæ are alike. Phylogenetic factors have not acted upon the stage, for we do not find several types corresponding to the several groups of the Gastropoda. The cause of the variations of the larvæ must then be sought for among other factors than phylogenetic, and, if this be so, the variations are not of taxonomic significance.

One of my critics has said (7): "No recent *Triton* has a protoconch*, such as is figured for this species (*T. radialis* Tate), by Mr. Kesteven (28), and I consider that it should be definitely separated from the species he has associated it with on this account alone, and most of the Australian Tertiary species will naturally fall into the same group." This dictum apparently affords a very striking illustration of the errors that may arise out of giving undue taxonomic value to the Protoconch. The writer in question was apparently under the impression that I had classed *Triton radialis* with recent species. Cossmann (6), one year later than myself, had proposed a new genus, *Austrotriton*, for the Tertiary forms referred to, and made *T. radialis* the type of the

* Pseudo-nectocoench—a cast of the Nectocoench, and formed during later stages than Phylembryonic.

genus. Dr. Dall was led by this to examine the species of Cossmann's genus, probably from figures only, and was satisfied that they formed a natural group, and he postulated from their adult similarity an apex for all, similar to that of *T. radialis*. It is to be regretted that he did not examine my group with more care, for, of the six species it contains, five are the Australian Tertiary fossils referred to by Cossmann; and I showed that, among these, there are at least four forms of protoconch, one of which is undeniably similar to that of the single recent species included.

Another example of the unreliability of the *Nectoco* as a taxonomic feature, is provided by the *Sinusigera* apex. In one of my first papers, I was led to expect that this apex would prove to be confined to species of the genus *Purpura*, but doubted whether it would be present in all the species of the genus (24). Mr. Iredale (22) has recently re-written "Kesteven's dictum thus: 'I do expect the embryo of every *Purpura* (or any other sectional name) (group?) to be of the *Sinusigera* type.'" He overlooked the fact that Baker (1) had described the apex of *P. lapillus*, in 1897, and that Pelseneer has studied the whole ontogeny, and that neither of these authors describes a *Sinusigera* apex for the species. In the same communication, Iredale records the presence of this apex in *Alectrion* (*Nassa*) and *Coralliophila*, whilst Mr. Hedley has described it in *Coralliophila* and *Bittium* (18). Here then is an exceedingly characteristic Protoconch, such as one was justified in expecting to prove taxonomically significant, but not only is it not present in all the members of any one genus, but occurs sporadically in at least four genera distributed over three families, one of which falls within the *Tenioglossa*, and two in the *Rachiglossa*, and of these latter one belongs to the subdivision *Glossophora* and one to the *Aglossa*.

It may be used neither to correlate nor to segregate.

The unreliability of the Gastropod *Phylembryo*, as represented by its *Nectoco*, for taxonomic purposes just demon-

strated, may be striking, but is no way unique, and is found equally in other invertebrate groups. Osten-Sacken (41), reviewing Portchinski's publications on the larvæ (*Phylembryos*) of Muscidæ, comes to the conclusion that: "The wonderful power of adaptation of these larvæ to their environment in a certain measure, destroys the parallelism we naturally expect to exist between the systematic characters of the larva and imago. . . . Distantly related species belonging to different genera issue from larvæ almost indistinguishable from each other. Again closely related and almost indistinguishable imagos, species of the same genus differ in their oviposition (size and number of eggs) and their larvæ follow a different law of development (as to the degree of maturity the larvæ reach within the body of the mother, the number of stages of development it passes through)."

It has been pointed out above that, although beyond the reach of phylogenetic influences of a minor kind (in the sense that they do not affect its morphological characters), the Gastropod *Phylembryo* and its *Nectoconch* are liable to a good deal of variation in form. In fact, the larval stages of this group of invertebrates, like those of many others, appear to have been especially susceptible to variation under conditions which do not affect the adult organism, so that there are marked differences in the larvæ of closely allied forms.

This phenomenon is of such common occurrence that Alfred Giard has been able to draw instances from nearly every group of animals, and discusses them under the name of Pœcilogony (9).

Is it possible to assign these variations of the Gastropod *Phylembryo* to any particular causes?

I am not in a position to offer complete explanations of any instance among the Mollusca, but certain observations which have been made on members of other phyla are suggestive, and perhaps capable of adaptation to instances among the Gastropoda. I give the observations first, and the explanations which they suggest for the Molluscan variations later, if

by their want of complete proof these suggested explanations stimulate investigation and criticism, then even if they prove wrong, they will have been productive of good.

1. A. Conte (5), after experimenting with the free Nematode, *Rhabditis monohysteria*, was enabled to record the following results: Grown on vegetable cultures, the worm was viviparous, or occasionally the ova were extruded in well-advanced stages of development, whereas grown in peptone, the worm immediately becomes entirely oviparous, and many of the eggs were in the two-blastomere stage. This extrusion of the ova was not simply due to stimulation of the germinative epithelium leading to distention of the oviduct and uterus, for whilst viviparous females were observed carrying over a hundred ova and a score of embryos, oviparous females carried only six to eight eggs. An oviparous female placed in vegetable culture rapidly became viviparous.

2. Giard (10), P. Mayer (38), and Boas (2) have put on record the fact that *Palæmonetes varians*, which lives at times in the sea and at others in brackish water estuaries and in branches of these which becoming cut off, are later converted into fresh-water lakes, presents two varieties according to its habitat. In one variety, the female, at the time of gestation, contains 321 eggs 0.5 mm. in diameter (*Microgenitor* Giard), the other (*Macrogenitor*) at a like period 25 eggs 1.5 mm. in diameter; and, further, that the ontogeny of the marine form, *Microgenitor*, is more extended than that of the fresh-water form, in which the eggs contain a more abundant nutritive yolk. Giard (9) states that a similar phenomenon is to be observed among related *Macrura*, when one is a fresh-water and the other a marine form.

3. *Alpheus heterochelès*, a *Macruran*, is, at Key West in Florida, hatched in the form of the adult; at the Bahama Islands, the young go through five ecdyses before attaining the adult form; whilst, at Beaufort in Carolina, the larvæ are hatched in a stage intermediate between these two (Herrick, 19).

In case No. 1, the Nematode, there can be no doubt that the different environments produce changes in the reproductive organs of the maternal organism, which, in turn, affect the life-history of the embryo, and the same may be said of case No. 2, *Palæmonetes*. In the case of *Alpheus*, the proof is wanting, but there can be little doubt that here also the variation in the ontogeny is due to environmental conditions acting through the maternal organism.

One form of the general question stated above is:—What explanation, other than phylogenetic, if any, may be offered for the fact that the protoconchs of nearly-related species present variations in the size of the caliculus* with resultant varying asymmetry and symmetry of initial coiling?

The caliculus of the *Nectocoenoch* was commenced by the Trochosphere before the asymmetrical growth of the larva began, and gives place to a coiled shell in the Trochosphere or early *Veliger* stage when the shell-secreting area partakes of the general asymmetry. Since the asymmetry of the larva appears very early, it follows that the caliculus is, in the majority of cases, formed before the larva is so far advanced as to take food, even where the whole larval development is intra-capsular, and the larva accordingly floating in a nutrient medium. Hence, the size of the caliculus is determined by the size of the egg; if that be large, the *Trochosphere* and early *Veliger* will be large, and so also the shell formed thereby.

If the plan of coiling be open and discoid, as, for instance, in *Spirula*, a large caliculus will not cause asymmetry thereof, but if, as in the example quoted, the larva fails to increase in size as rapidly as when secreting the caliculus, then that

* This term is introduced here for convenience and precision of description and argument. It is applied to the bilaterally symmetrical thimble- or saucer-shaped nucleus which forms the starting point of all protoconchs. It differs in character from the conchogenetic terms proposed earlier inasmuch as it applies to a particular portion of the protoconch formed at any stage of development, not to any portion formed during a particular stage.

will have a larger diameter than the succeeding whorls. If, on the other hand, the plan of coiling of the shell be a close spiral without an umbilicus, then if the conditions found in *Spirula* are present, the caliculus must be placed more or less eccentrically.

Whence it may be stated that a large caliculus placed eccentrically, owes its origin and eccentricity to (1) the size of the egg and larva during its formation, and (2) the rate of growth of the larva subsequent to its formation.

Isolated examples of the condition in question could probably be found in almost every genus among the Gastropoda; to attempt to make a complete list would serve no good purpose. I give but a few typical instances:—*Scaphella (Voluta) mamilla* Gray, *Columbella australis* Gaskoin (26), *Cymatium (Triton) woodsi* Tate and *C. radiale* Tate (28), *Megalatractus aruanus* Linn. (31), *Triphora labiata* A. Adams (13), *Mangelia lutraria* Hedley (14), *Cerithiopsis haligani* Hedley (15), *Thetidos morsura* Hedley (16), *Turricula pilsbryi* Hedley (*loc. cit.*), *Syrnola macrocephala* Hedley (17), *Mathilda decorata* Hedley (*loc. cit.*), *Cerithiopsis cacuminatus* Hedley and Petterd (18), *Pleurotoma casearia* Hedley and Petterd (*loc. cit.*), *Terebra lauretanae* Tenison-Woods (*loc. cit.*). This list might be further added to without going outside the limits of my own library, which is quite small. Two facts stand out from it—(1) that the large apex occurs in genera in which, as a rule, the apex is small and quite symmetrical; (2) that it occurs more frequently in deep water than in littoral forms.

The above are instances of a particular kind of apex arising out of particular and recognisable morphological features of ovum and larva, but, as yet, no explanation has been offered for those morphological features; that explanation may perhaps be extracted from the following observation by Sturany. In *Fusus bifrons* and its variety *paucicostata* two types of protoconch occur; in the type, which inhabits shallow coastal waters, the protoconch is small: in the variety, which

is an inhabitant of deep waters, it is large. Similar phenomena have been recorded for *Murex tribulus* and *Sipho gracilis*. Boettger has collected these together under the name of "Hétérostylie," and has expressed the opinion that: "It seems indeed that the embryos of a single genus are able to undergo a kind of adaptation, and that this differential character, far from recalling an ancestral form, appears as an accommodation entirely secondary."

That the variation is due to environmental conditions, seems at least exceedingly probable, in view of the phenomenon presented in *Palæmonetes varians*. In this case, the primary factor responsible for the variation was undoubtedly the alteration in the concentration of the salts in the water. This may have acted only through the resultant change in osmotic pressure, but more probably through the change in concentration and relative proportion of the individual salts (see Loeb, 36, 37; Ringer, 43; and W. A. Osborne, 39, 40); and also, perhaps, by the change in foodstuffs, for the change in saline contents of the water would exterminate some members of the related fauna and flora, and allow of their replacement by new forms.

I would explain the large Gastropod Protoconch as resulting from a modification of the mode of production, induced by some new condition in the environment, and leading to an increase in the size of the ovum and perhaps also, in some cases, an increase in the intra-capsular nutrient material. The former would determine a large thimble-shaped nucleus, and the latter permit a maintenance of the rapid growth of the larva whilst still within the egg-capsule. In the deep water forms it is probable that the *Veliger* stage is passed within the egg-capsule. As causative factors in the case of *Fusus bifrons*, etc., we may point to the difference in pressure, and the attendant difference in saline contents of the water.

Such an explanation as the above is not available for such bizarre forms of the protoconch as, for instance, the *Sinusi-gera*; but, in these, it is probable that a study of the living

Veliger will reveal the fact that the sinuation of the outer lip is referable entirely to mechanical factors, and that the weight of the calcareous shell is to a large extent responsible; such sinuations do not occur in horny *Nectocoenchs*.

A failure to realise the fact that these variations are not of phylogenetic significance has resulted in errors on the part of the taxonomist. I was myself responsible for Mr. Hedley's description of immature *Coralliophila lischkeana* Dunker, under the name of *Purpura sertata* (17), on the evidence of the *Sinusigera* apex, an error which his more recent discovery of the adult shell from nearly the same locality has enabled him to correct (18). Similarly believing that the size of the symmetrical thimble-shaped nucleus of the protoconch (*caliculus*) was of phylogenetic significance, Dall used it for taxonomic purposes when he advocated the retention of Cossmann's genus *Austrotriton*, although, as noted above, he was apparently satisfied that, as judged by adult characters, the type of the genus was rightly placed with forms developed from smaller eggs, and, therefore, possessing the normal symmetrically coiled protoconch of the genus *Cymatium*.

Of the disproportionately large apex discussed above, three varieties are recognisable, the first or *Mamillate* is typified in *Scaphella mamilla* Gray, and gives its name to the species; the second or *Eccentric* is typified in *Megalatractus aruanus* Linn., and *Cymatium woodsi* Tate; the third or *Tumid* apex is typified in *Terebra lauretana* Ten. Woods, and *Syrnola macrocephala* Hedley, and is responsible for the specific name of the last. In the first and second types, the characters are in the *caliculus*, in the third type rapid growth throughout the *Veliger* stages produces a large symmetrical *Nectocoench* of two or more whorls. It has already been suggested that this rapid growth is due to the presence of a large amount of nutritive material within the egg-capsule. This suggestion is supported by the fact that, in those cases which I have been able to study directly, as in those of which I find information in literature, the whole of the larval stages are

passed within the capsule. This leads to the suggestion that, in all those cases where a calcareous protoconch of but few large whorls is present, the whole of the larval stages are passed within the egg.

The converse of this, however, does not hold true; there are very many species which pass the larval stages within the capsule, and which do not possess *Tumid*, *Mamillate* or *Eccentric* apices; such is the case throughout the Pulmonata and in *Littornia*, *Purpura lapillus*, *Vermetus* and many *Murices*. *Paludina* and many Pulmonates are viviparous, as indeed are some species of *Littorina*, if not all; and, in all these cases, the apex is perfectly regular.

The abundance of nutrient material within the capsule does not, of necessity, determine a tumid apex; in *Purpura lapillus* Linn., and several other species, the few embryos which escape from the capsule have previously eaten the many others originally present in it. In *Megalatractus aruanus* Linn., there is sufficient food-material to support the embryo whilst forming five or six whorls of (ananeanic) shell, but the apex is *eccentric* in this species, not tumid.

“A number of the species (of *Cymatium*) have a world-wide distribution, which is doubtless due to their free-swimming pelagic larvæ (Tryon). I am inclined to carry this statement further, and to say that the distribution of a species is largely decided by the size of its protoconch.” The above is a quotation from my paper on “*Litorium*,” and needs modification. I had been struck by the fact that most of the many-whorled protoconchs occurred in species of wide distribution, whilst the localised species had, in general, small protoconchs. In the case of the species of *Cymatium*, the generalisation is justifiable; the protoconch is the replica of the *Nectoconch*, that is to say, the number of whorls in it is a measure of the length of the pelagic existence of the species. Beyond the genus *Cymatium*, the generalisation, as expressed above, is liable to lead erroneously to its own refutation. Stated so as to be generally applicable, the idea which the above statement

was intended to embody is as follows:—In as far as the size of the protoconch is a measure of the length of the pelagic existence of the species forming it, so also will it be, in most cases, a measure of the distribution of the species. This mode of expression of the idea becomes necessary with the discoveries that a protoconch may be largely ananeanic, post-larval, and that in some cases, *e.g.*, *Triforis*, several of the early whorls of the shell, differing only in size from all which succeed them, may have been formed by the larva.

THE HETEROSTROPHE APEX.

The Heterostrophe Apex is of particular interest, because it apparently stands out as an apex which is perfectly trustworthy for taxonomic purposes; examination of the facts shows, however, that the heterostrophic apex is confined neither to a single genus nor indeed to a single family; and, moreover, that it is not constantly present in the species of the several genera in which it has been described as a diagnostic character, *e.g.*, *Eulima*. It was on this evidence that Tate and May assigned to the Pyramidellidæ their new genus *Pseudorissoina* of which they say: "Briefly this new genus is a Pyramidellid with a Rissoina aperture or a Rissoinid with a Pyramidelloid nucleus (apex)." They also say that it has the "spire and aperture of a Rissoina, and are induced by" the higher value of the nuclear character (over adult characters) in classification to place it, in Pyramidellidæ, near *Eulimella*." I would not be understood to say that this classification is wrong; that question must remain until the mollusc itself is known, but I would point out that it is based on a wrong premise.

The heterostrophic character has arisen out of a twisting of the mollusc in the shell. This may be illustrated by a reference to *Risella* and *Littorina*. In the former genus, the dorsum of the body is related to the lower aspect of the penultimate whorl, and the retractor muscle attached to the floor of the ultimate whorl. In *Littorina*, the dorsum of the body is

related to the outer aspect of the last whorl, and the muscle attached to the columella (28).

Suppose now, in the latter form, the mollusc, already in possession of all its adult characters, becomes rotated within the shell through an angle of 90° , so that the dorsum be related to the lower wall of the ultimate whorl, as is the case in *Risella*, the shell subsequently formed will have its axis at right angles to that of the portion formed before the rotation, and there results a dextral heterostrophic apex. In the true *Heterostrophe* apex, the process is further complicated by the sinistral coiling of the shell previous to the rotation.

In the *Anastrophic apex* (*Solarium*), there is a simple change from sinistral to dextral coiling without any rotation within the shell; had such occurred in the elongated, closely-coiled *Eulimoid* and *Pyramidelloid* species, then in these also the axis of the apex would have been that of the adult shell, and the latter would be wound round the sinistral apex. The heterostrophic apex then may be said to have resulted from two factors, a sinistral apex, and growth of the dorsal portion of the body so much in excess of the ventral as to preclude an open coiling of the shell, such as would permit the inclosure of the sinistral portion on the assumption of the dextral coiling, and this latter evoked a rotation within the shell. It is interesting to note that, even in those heterostrophic apices of one whorl, which would not have interfered with a dextral coiling without rotation, the rotation has nevertheless occurred.

THE ANANEANOCONCH.

In view of the demonstrated fact that some protoconchs are formed in part subsequent to the nepionic stage, such protoconchs are of varying significance. Two more or less sharply differentiated types of *Ananeanoconch* are recognisable; those which form the initial portion of the true conch, and present more or fewer of the adult characters; and those

which, being moulded inside the horny *Nectocoench*, are devoid of the adult characters; for these latter I used the term *Pseudo-Nectocoench* (*ante* p. 62); in such instances the *Ananeoconch* of the former type is also present.

The *Pseudo-Nectocoench* will generally have smooth and rounded whorls; since such is the character of the inside of the majority of the horny *Nectocoenches*, they, in many instances, present a complete model of the inside of the *Nectocoench*; in others, they fall short of this, owing to the interposition of a septum between the upper and lower whorls; this deficiency reaches its maximum in those cases where the whole *Nectocoench* is shed, and the apical whorl closed by a shelly septum (*caducous apex*).

Ananeoconchs of the former group often present interesting features. In the generality of cases, the *Ananeoconch* presents the contour and sculpture of the adult shell; such is the case throughout the genus *Cymatium*, including most of those segregated by Dall under the name *Septa*, and with only one or two exceptions. In a few cases, however, we find the *Ananeoconch* presents characters differing in some marked way from those of the adult, presenting, in fact, examples of *adolescent poecilogony*, when we compare allied species. The most striking instance I know of among the Mollusca, is one which I myself recorded in "A Note on Two Species of *Astralium* from Port Jackson" (26). In this case, two species, so similar to one another that they had not previously been recognised as distinct, were shown to have *Ananeoconchs* presenting different types of coiling; the one being truly trochiform, with columella and no trace of umbilicus; the other, at the same stage, is *Liotia*-like, with a wide umbilicus.

At that time I offered the opinion that: "These two species would seem to present an exception to the rule that distinctive characters are inherited earlier in successive generations, for, by that theory, *A. fimbriatum* should be descended from

discoid ancestors, whilst *A. tentoriforme* should come from trochiform ancestors."

I have now no doubt that such a conclusion is at fault. I would say rather that the former species was truly intermediate between the trochiform and the open-coiled species of the *A. imperiale* type, and that, in its early *Neanic* stage, it carries traces of an ancestry common to both, but whose track is already eliminated from the ontogeny of *A. tentoriforme*.

Another instance of an interesting neanic shell, which, in this case, owes its form to its ancestry will be found below, in the account of the probable course of the evolution of *Cymatium parkinsonianum* Perry, from the Tertiary species, *C. tortirostris* Tate.

Boutan has discussed the phylogenetic significance of the stages in the ontogeny of *Fissurella*, and his figures have been reproduced in several places. It is interesting to note that the embryonic stages which he figures have been fixed, as it were, in other genera.

On Plate i., a series of retouched photographs of *Cymatium parkinsonianum* Perry, and *C. tortirostris* Tate, are reproduced; similar photos. of *C. abboti* Tate, are also reproduced for comparison with these. The interest attached to these shells is that *Cymatium parkinsonianum* is apparently the recent form of *C. tortirostris*. The typical form of the latter (fig. 2) retains its nodulose ribs and well-developed revolving liræ throughout. In the variety (fig. 1), which has the same outline as the above, the revolving liræ are obsolescent on the last half of the body-whorl, and the last few ribs are less nodulose. In *Cymatium parkinsonianum* (figs. 5-8), the early (*neanic*) whorls are heavily lirate and nodulosely ribbed (fig. 8), exactly resembling the early whorls of the typical *Cymatium tortirostris*, but in the last three whorls the liræ are reduced in size and the ribs not nodulose. The contour is that of *C. tortirostris*. The main difference between the two (for the species are alike), is that, in the recent form, the reduced sculpture appears earlier in the shell. The recent

form has evolved from the Tertiary by the continuous tachygenetic inheritance of this reduction in the power to form a heavily sculptured shell. (*C. parkinsonianum* is the recent species I associated with *C. radiale* Tate, *C. tortirostris* Tate, *C. abboti* Tate, *C. textile* Tate, and *C. woodsi* Tate, and all have the same contour and general appearance as the three figured here.)

The general conclusions arrived at are:—

1. The Gastropod Protoconch may have been formed during one or more of four stages in the ontogeny of the mollusc.

2. The common practice of speaking of the early portion of the true conch as *Nepionic*, is wrong; it would be more correctly designated *Ananeanic*.

3. The *Nepionic* stage in the Mollusca, at least in the Gastropods, is exceedingly brief; and, in the great majority of cases, leaves no conchylaceous record.

4. As a taxonomic feature, the protoconch is practically worthless, and is liable to be, and indeed has proven, very misleading.

5. This is owing to the fact that its various forms have arisen from factors other than phylogenetic.

6. The absence of definite types of *Veliger* larvæ corresponding to the main divisions of the Gastropoda, is very strong evidence that phylogenetic factors have not acted upon this stage of the gastropod ontogeny (and it is during this stage that the vast majority of protoconchs are formed).

7. By reference to phenomena observed (and more or less explicable) in other Phyla, much light is thrown upon the variations of the Gastropod Protoconch.

8. The Heterostrophe apex has arisen from two factors: (*a*) the initial sinistral coil; (*b*) the much more rapid growth of the dorsal region of the body than the ventral, preventing an open coiling such as would permit of a simple assumption of dextral coiling by enclosing the sinistral portion as in the anastrophic apex.

9. The combination of these two factors has caused the mollusc to rotate through an angle of 90° within its shell, thereby coming into a position in which the close spiral might be maintained.

10. The *Mamillate*, *Eccentric*, and *Tumid* Protoconchs will generally be found to be correlated with an absence of free pelagic existence; the converse, however, will not hold true; the absence of these types of protoconch does not necessarily indicate a free pelagic *Veliger* stage.

11. The distribution of marine species has been determined, in large measure, by the length of the pelagic existence of the *Veliger*; and hence in as far as the size of the protoconch, number of its whorls, etc., is a measure of the length of the pelagic existence, so also will it be in many cases a measure of its distribution.

12. The characters of the *Ananeanoconch*, or that portion of it which constitutes the first whorl or two of the true conch, may often be used to outline the more recent evolution of a species.

THE GENUS *SEPTA*.

In the paper above referred to, Dall (7) separates those species of the genus *Cymatium* which resemble *Cymatium tritonis* Linn., under the name of *Septa*, giving the name full generic rank. He says (p. 126): "In considering the arrangement of the members of the group (Frog-shells and Tritons) the dentition, the protoconch and nepionic shell, and the generic rank. He says (p. 126): "In considering the arrangement, and with the possible exception of the last all are more important than conchological (conchic?) sculpture and form." The meanings of the terms "protoconch" and "nepionic shell" as used by him are peculiar; it appears that he differs from all other conchologists and malacologists in restricting the term protoconch to the *caliculus*, and applies the term "nepionic shell" to the remainder of what is usually termed protoconch. This interpretation of his meaning is drawn

from the following statement:—"The protoconch and nepionic shell in the Tritons are practically continuous and inseparable. . . . The nuclei of the Australian fossil forms, as figured by Kesteven (27), indicate that a protoconch, as distinguished from the nepionic shell, was present in some if not all these forms." From this it follows that his interpretation of the term *Neanic* is the same as mine; he applies it to the early whorls of the true conch.

Dr. Dall's justification for the segregation of these species from the rest of the genus rests upon their supposed possession of three characteristics, viz. :—

1. "*Septa* is separated from the other Tritons by its laterally extended rachidian tooth with a median inflexion in front, but without basal plates, recalling that of *Cassis*."

2. "The operculum of *Septa* has it (the nucleus) subcentral and internal."

3. "In one group alone, *Septa*, is there a distinctly marked neanic stage." "The larval shell of *Septa* is identical in general characters (with those of other members), but is followed by a neanic stage in which the elegant granular sculpture, and delicate rose colour of the test contrast effectively with the features of the adult, though there is no very pronounced line of demarcation between the two."

A generic segregation, or in fact any segregation, of a group of species can be justified only on one or both of two grounds. The features relied upon for the segregation must be either of Phylogenetic significance, or else they must be of such a kind as to minister to the convenience of the Taxonomist, and the science generally through a more or less artificial classification.

Only one of the above features has any real claim to be regarded as of phylogenetic significance, namely the character of the radula; the value of this, as of most other characters for taxonomic purposes, is to a certain extent determined by the personal factor, but I would point out that the differences between the radulæ of *Cymatium cutaceum* Linn., and

Cymatium tritonis Linn., (the most dissimilar pair of radulæ as yet known in the genus) are much less than the differences between the radulæ of *Megalatractus aruanus* Linn., and *M. maximus* Tryon (*vide* 31), and that in this case there can be no doubt that the two species belong to the one genus. Other comparable pairs of species might be quoted to show that radular differences of these small orders are devoid of Phylogenetic significance.

Turning next to the operculum, Dr. Dall very correctly suggests that this is possibly of less value taxonomically than adult conchic characters. It is, however, interesting to note that Dall's definition of the operculum in *Septa* does not apply to that of the type of the genus (?), *Septa rubicunda* Perry, which has the nucleus of the operculum subapical and marginal. In old and large specimens a few perfectly concentric laminae remove the nucleus from the margin, but even in these it would be quite erroneous to describe it as "sub-central and internal."

Thirdly, the possession of a distinctive *Neanie* shell is neither confined to the *Septa*-group nor present in all its members. The type of the genus (?) shows no such stage, neither do *C. pumilio* Hedley, *C. petulans* Hedley, nor *C. bassi* Angas, whilst *C. parkinsonianum* Perry, has a neanic stage even more marked than that of *C. tritonis* Linn.

I have dissected *Cymatium spengleri* Chemnitz, and *C. (Septa) rubicunda* Perry, side by side, carefully comparing each stage of the dissection, and I fail to find any points of anatomical difference worthy of note beyond the radulæ.

We are thus once more driven back to the adult shell as our final guide in any arrangement of the members of the genus, and here all the evidence points to the complete homogeneity of the group.

Hedley recently described a new *Cymatium (petulans)*, and, adopting Dall's division of the genus, he placed it in *Septa* "from the general resemblance it bears to *S. tritonis* Linn." (18). In 1903 (17), he described *Lotorium pumilio*; this also

he has since placed in the genus *Septa*. When describing *C. pumilio* he wrote: "The nearest relation is *L. bassi* Angas, with which it agrees in the small number of its whorls, colour, sculpture and general appearance." After comparing—at my request—*C. petulans*, *C. pumilio*, and *C. parkinsonianum*, Mr. Hedley expressed the opinion that, in the adult shells, there were no features on which to divide these species generically. *C. parkinsonianum* finds no place in my "tritonis group" (27), that is in the genus *Septa* Perry-Dall.

Whilst adopting my "groups" of the genus *Cymatium*, Dall differs from me in that he has given these groups quotable names, assigning them varying sectional values. When one remembers the divergence of opinion in the past among authors, in assigning the species to the various groups, such a procedure seems rather courting confusion, for the adoption of the sectional names would lead to many species being assigned now to one section, now to another. On one other point does Dr. Dall differ from me; he proposes to separate my "group of *C. quoyi*" from *Cymatium* as a full genus under the name of *Personella* Conrad. To those familiar with the species of the group, such a proceeding would not seem desirable or justifiable. Hedley recently described a "*Cymatium columnarium*," which, he says, "stands nearest to *C. quoyi* Reeve, from which it differs by being thinner, more slender and with weaker sculpture." Dr. Dall (*sub voce Personella*) writes: "Type *P. septemdentata* Gabb. Eocene. Recent analogue, *Triton quoyi* Reeve." Hedley (l.c.) refers to Dall's proposition, but does not assign his species to *Personella*.

Dall is undoubtedly correct, in considering that, in the arrangement of the members of this group, "the dentition, the protoconch and nepionic shell and the operculum must all be considered," also that adult conchic characters are not altogether devoid of taxonomic value. Of these four characters, the operculum is neutral, the protoconch and nepionic shell, and the adult conchic characters point to the natural

character and unity of the genus; the dentition alone remains to justify any splitting of the genus, but to do so is to fail to consider all four characters.

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EXPLANATION OF PLATE I.

Figs. 1-2.—*Cymatium tortirostris* Tate.

Figs. 3-4.—*Cymatium abboti* Tate.

Figs. 5-8 —*Cymatium parkinsonianum* Perry.

Figures 1 to 7 are photographs which have been carefully re-touched under a lens; figure 8 is reproduced from my paper, “The Protoconchs of certain Port Jackson Gastropods,” published in 1902.

The specimens of the fossils were kindly lent me from the Australian Museum Collection, by Mr. R. Etheridge, Jr., Curator, and to him my thanks are tendered.